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PARENT-SPECIFIC GENE EXPRESSION AND THE TRIPLOID ENDOSPERM

The endosperm of flowering plants is a tissue that acquires resources from the maternal sporophyte and is in turn digested by the developing embryo in its own seed. In this respect, the endosperm takes the role filled by the female gametophyte in gymnosperms. Endosperm is a tissue unique to angiosperms. At fertilization, a male gametophyte (pollen tube) releases two sperm into the female gametophyte. One sperm fuses with the egg to form a diploid zygote, and the other sperm fuses with two female-gametophyte nuclei (known as polar nuclei) to form the triploid primary-endosperm nucleus. Therefore, the endosperm, which develops from this triploid nucleus, has an unusual genetic composition. Each nucleus contains one copy of the paternal contribution to the associated embryo and two copies of the maternal contribution. A minority of flowering plant species have endosperms of different genetic composition, but almost all share the characteristic that more of the endosperm genome is derived from the mother than from the father.

Double fertilization and the formation of endosperm are often considered the major features that distinguish flowering plants from other seed plants. Because of this importance, many authors have suggested adaptive explanations for the unusual genetic constitution of endosperm. Heterozygote vigor (Brink and Cooper 1940) can explain the presence of a paternal contribution but not why the maternal contribution should be doubled. Polyploid vigor (Stebbins 1974) can explain the advantage of triploid over diploid endosperm but not the weighting toward the maternal contribution. In other words, the polyploid-vigor explanation does not explain why genome doubling should occur in the female gametophyte before fertilization, particularly given that endosperm cells often increase their ploidy by other means after fertilization (D'Amato 1984).

More-recent hypotheses have treated the endosperm as a participant in conflicts of interest among mother, father, and offspring. Conflict arises because sibling offspring of one mother tend to compete with each other. Each offspring's prospects of survival and eventual reproduction are sensitive to the quantity of resources it obtains from the mother, and when some offspring obtain more resources, others tend to obtain less. Because the mother is equally related to (has an equal genetic investment in) each of her offspring, her inclusive fitness is greatest when all nonabortive offspring are provisioned equally (Smith and Fretwell 1974; Trivers 1974). However, each offspring is more closely related to itself than to its siblings. For this reason, individual offspring would benefit from some redistribution of the mother's resources toward themselves and away from their

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sibs. In this sense, there is a conflict of interest over resource allocation between each offspring and the mother. The fact that offspring are more closely related to themselves than to their sibs arises in part because they carry genes from different fathers. To this extent, the conflict of interest between a mother and each offspring is also a manifestation of conflict between the mother and the father over resource allocation.

Charnov (1979) suggested that double fertilization functions to shift the genetic interests of the resource-acquiring tissue toward the father's or embryo's interests and away from the mother's interests. The relevant coefficients of kinship have been calculated (Westoby and Rice 1982; Queller 1983; Willson and Burley 1983), and the authors have argued that the endosperm's interests should in some sense be intermediate between those of the mother and the embryo and between those of the mother and the father. In consequence, the endosperm should behave differently from both the embryo and the mother with respect to acquiring resources at the expense of siblings.

In contrast, Law and Cannings developed an explicit genetic model not based on kinship coefficients and concluded that "the addition of a second polar nucleus (identical to the first) makes no difference to the fitness of maternal sporophyte or embryo sac" (1984, p. 67). Queller (1984) presented a different genetic model, in which the behavior of triploid endosperm was consistent with predictions based on kinship coefficients. The difference between the two models has two basic causes. First, Law and Cannings considered only alleles that were dominant or recessive or had threshold effects. Queller also considered alleles with additive effects. Second, and more important, in Law and Cannings' model the costs associated with overconsumption by some endosperms were experienced solely by underconsuming endosperms within the same brood. In Queller's model, the cost of overconsumption in the current brood was experienced as reduced resources for offspring in subsequent broods. Therefore, the cost was experienced by both underconsuming and overconsuming genotypes.

We present a model for the evolution of triploid endosperm from a diploid "endosperm" containing a single genome from each parent. This is best understood as a purely formal device to show that the double maternal dose can have a significant effect on gene expression. However, demonstrating a selective advantage for maternal doubling in the context of such a diploid "endosperm" may have phylogenetic implications. The resource-acquiring tissue in gymnosperms is the female gametophyte. Triploid endosperm differs from a female gametophyte in two respects. A paternal genome is added, as is a second maternal genome identical to the first. Logically, the addition of a male genome to a gametophytic nucleus other than the egg (double fertilization) could have preceded doubling of the maternal genome, or vice versa. Our model indirectly suggests that double fertilization is more likely to have preceded maternal doubling than the other way around.

It should be emphasized, however, that our model does not directly address the phylogenetic issue. Rather, it addresses the question arising from the literature summarized above: why should a triploid endosperm behave differently from a tissue with a single maternally derived genome, considering that the triploid endosperm's genotype is qualitatively (though not quantitatively) identical?

PARENT-SPECIFIC GENE EXPRESSION

We propose a mechanism whereby the maternal loading in the 2:1 endosperm could generate a tissue that behaves differently with respect to resource acquisition than would a hypothetical 1:1 endosperm. The mechanism we propose requires that an allele have different expression depending on its parent of origin. This contrasts with the traditional assumption that an allele's expression is independent of whether the allele is derived from the mother or the father.

Recent advances in mouse embryology and molecular biology have demonstrated that the traditional assumption must be rejected in at least some cases. Maternal and paternal genomes are both necessary for normal development in mice, and this is believed to account for the absence of parthenogenesis in mammals (Surani 1987). Mouse embryos formed from two male pronuclei have larger trophoblasts than do normal embryos or embryos formed from two female pronuclei (Barton et al. 1984). The trophoblast is the offspring tissue directly involved in nutrient transfer from the mother. Mouse neonates with both copies of chromosome 11 derived from their mother are smaller than normal litter mates, whereas neonates with two paternal copies of chromosome 11 are larger than normal litter mates (Cattanach and Kirk 1985). These observations are consistent with greater activity by paternally derived alleles in acquiring resources. In addition, differences have been detected in methylation and gene expression between maternally and paternally derived chromosomes (Reik et al. 1987; Sapienza et al. 1987; Swain et al. 1987). We refer to all cases in which an allele has a different phenotypic effect depending on its parent of origin as parent-specific gene expression (PSGE). Evidence for PSGE in endosperm will be discussed in a later section.

Why should natural selection favor alleles that are more active in acquiring resources from the mother when paternally derived than when maternally derived? If other offspring of the mother sometimes have different fathers, there is an asymmetry between the interests of an offspring's alleles that are derived from its father and the alleles that are derived from its mother. A paternally derived allele will be absent from maternal half sibs, but a maternally derived allele will be present in 50% of these half sibs. Paternally derived alleles should be selected to acquire more resources than maternally derived alleles, because resources acquired by the offspring should tend to reduce a mother's expectation of reproductive success through other offspring. This reduction imposes greater costs on the overall transmission of maternal alleles than of paternal alleles.

Of course, it is not always the case that alleles expressed in offspring can influence the amount of resources acquired from a parent. In most oviparous animals, egg size and egg contents are determined before alleles expressed in offspring can have any effect. The requirements for PSGE are met only for organisms in which the offspring genotype is active while the mother is supplying resources. The obvious example occurs in viviparous species, such as eutherian mammals. In contrast, there is no scope for the evolution of PSGE in pelagic-spawning fish, because fertilization is external and there is no subsequent parental care. These considerations might explain the distribution of parthenogenesis among vertebrates. Parthenogenesis occurs in all major groups of vertebrates

except mammals. Surani (1987) and others have suggested that parthenogenesis is impossible in mammals because both a paternal and a maternal genome are required for normal development. PSGE may be absent from vertebrate groups with parthenogenetic members.

APPLICATION OF PARENT-SPECIFIC GENE EXPRESSION TO SEED PLANTS

The necessary conditions for PSGE are met in flowering plants, though here the resource-acquiring tissue is often triploid endosperm rather than a derivative of the diploid zygote. In this section we speculate how selection for PSGE might favor a triploid endosperm over a hypothetical diploid produced by double fertilization.

Our hypothesis supposes that natural selection is acting on the level of the transcription of genes. A gene can be considered to consist of a transcribed coding sequence and nontranscribed control sequences that determine the level of transcription. In effect, we consider cases in which selection operates on the control sequences, without affecting the coding sequence.

First, let us consider selection in a diploid resource-acquiring tissue that is genetically identical to its associated embryo. Consider a gene encoding a protein that acquires resources from the mother. Assume that initially there is no PSGE, that all copies of this gene are initially transcribed at some level x that is independent of parental origin. The total transcription of genes at this locus in the diploid tissue will be $2x$. This level of transcription is subject to natural selection, and therefore, under the assumption of no PSGE, $2x$ is expected to be optimal from the perspective of an allele that is as often maternally derived as paternally derived.

However, from the perspective of the paternal allele expressed in offspring, the optimal level of transcription would be greater than $2x$. It would be greater for the reason outlined above: briefly, the other individuals that would suffer deleterious effects from an individual offspring's acquiring more resources would be less likely to carry the offspring's paternal allele than the offspring's maternal allele. Let the optimal level of transcription for a paternally derived allele be $2x$ plus some amount y. By the same token, the optimal level of transcription for a maternally derived allele would be $2x$ minus some amount z. In other words, for alleles of this type and in the absence of PSGE, the achieved level of transcription, x, should be a compromise between the different levels that are optimal from the perspectives of paternally derived and maternally derived alleles.

Now, suppose that PSGE is possible, thus allowing mutant alleles that are transcribed at one level when maternally derived but at a different level when paternally derived. Specifically, consider a mutant that is transcribed at level x when maternally derived but at level $x + y$ when paternally derived. The new allele would initially be present in heterozygous diploid endosperms with total transcription $2x$ when the allele is maternally derived but with total transcription $2x + y$ when the allele is paternally derived. Such a mutant would be able to invade a population fixed for transcription level x because, from the perspective of a paternally derived allele, $2x + y$ is a better level of transcription than $2x$. By a similar argument, an allele that has transcription level $x - z$ when maternally

derived but transcription level x when paternally derived could also invade a population fixed for transcription level x.

Thus, given that PSGE is practicable in a biochemical sense, we would expect populations fixed for transcription level x to be invaded by alleles with higher transcription when paternally derived, with lower transcription when maternally derived, or with both. At what transcription levels would this selective process be expected to stop?

Clearly, the optimal transcription level for the paternally derived allele at a locus depends on the number of transcripts produced by the maternally derived allele, and vice versa. As the transcription of paternally derived alleles increases under the influence of natural selection, the optimal transcription level of maternally derived alleles decreases. Provided that transcription of the paternally derived allele is not constrained below $2x - z$, the evolutionarily stable state will be zero transcription of the maternally derived allele. All transcription at the locus should be of the paternally derived allele. Therefore, the model predicts the existence of a group of loci (here, class-A loci) with paternal expression only. Remember that the argument thus far deals only with loci that encode proteins directly involved in acquiring resources from the mother. All class-A loci would be of this type.

Our argument aims to explain how it could come about that a triploid resource-acquiring tissue would behave differently from a diploid one, even though no different alleles were present. The model thus far, which considers only class-A loci, cannot explain differences in expression at these loci between triploid and diploid resource-acquiring tissues. This is because the triploid tissue differs only in containing an extra dose of the maternally derived allele; and because maternally derived class-A alleles are predicted to have zero expression, the extra dose would make no difference.

However, the addition of an extra maternal dose would affect the expression of class-A loci, if two additional assumptions are made: (1) there are other loci, essential to offspring fitness, that do not acquire resources from the mother and are not subject to selection for PSGE (class-B loci); and (2) the level of expression of class-A loci is not independent of the level of expression of class-B loci. Specifically, we assume that high levels of expression of class-B loci reduce the expression of class-A loci. This would result from competition between loci for nucleotides or polymerases during transcription or from competition between transcripts for amino acids, ribosomes, or tRNA's at the stage of translation into protein.

Given these assumptions, the effect of doubling the maternal dose in triploid endosperm is to reduce the expression of class-A loci. Let the total transcription at all class-A loci be P and the total transcription at all class-B loci be $2Q$. Therefore, the total transcription of a diploid resource-acquiring nucleus is $P + 2Q$, and the proportion of transcripts that come from class-A loci is $P/(P + 2Q)$. Now compare the diploid tissue with a triploid endosperm. Transcription at class-B loci is now $3Q$ and the proportion of class-A transcripts is $P/(P + 3Q)$. Provided that Q is substantial relative to P, the effect should be to reduce transcription (or translation) of class-A loci.

In summary, a triploid resource-acquiring tissue could be expected to transcribe

resource-acquiring loci at a lower level than a diploid resource-acquiring tissue, given selection for PSGE and some competition for transcription between resource-acquiring (class-A) and other (class-B) loci. In this sense, a triploid tissue would behave in a manner closer to the genetic interests of the maternal sporophyte and the female gametophyte. This, in turn, could explain why natural selection might produce doubling of the maternal genetic dose in endosperm.

TESTABLE FEATURES OF THE HYPOTHESIS

The hypothesis outlined above relies on the standard assumptions of evolutionary theory, that natural selection acts on the phenotypic consequences of alleles expressing themselves in particular tissues and that the direction of selection can be predicted by considering how different phenotypic characteristics of a tissue would affect the frequency of the responsible alleles in future generations. Beyond this generality, the hypothesis makes some more particular assumptions or predictions, and it is open to falsification by testing these. There are two major assumptions.

1. Biochemical mechanisms exist by which parent-specific gene expression could be brought into existence, if natural selection favored it.
2. Resources available for gene expression are restricted at the level of whole genomes, such that the increased expression of one set of loci implies a decreased expression of some other set.

The major prediction of the hypothesis is that there exists a class of loci for which paternally derived alleles are considerably more strongly expressed than maternally derived alleles. These loci are predicted to encode proteins responsible for acquiring resources from the mother for the offspring, and the PSGE in question should be found in the offspring tissue that acquires resources.

SOME SUPPORTING EVIDENCE

Parent-specific gene expression has been reported from maize endosperm (Kermicle 1970; Lin 1982, 1984). Endosperms that lack a paternal copy of the long arm of chromosome 10 produce small kernels. Kernel size is not restored by adding extra maternal doses of 10*L* (Lin 1982). This is direct evidence that there exist gene loci on 10*L* that are preferentially expressed when paternally derived.

In a series of elegant crosses, Lin (1984) produced maize endosperms with either one or two paternal genomes and from one to eight maternal genomes. The only combinations that produced normal endosperms were two maternal genomes to one paternal genome and four maternal genomes to two paternal genomes (2m:1p and 4m:2p). This suggests that a ratio of two female genomes to one male genome is necessary for normal endosperm function. Two classes of tetraploid endosperm were produced. Endosperms with 3m:1p produced small kernels, whereas those with 2m:2p were aborted. For endosperms with 3m:1p, our hypothesis predicts that the extra dose of maternal class-B genes should further dilute the resource-acquiring activity of class-A paternal genes. Thus, the small size of these endosperms is consistent with our hypothesis. Similarly, our hy-

pothesis might predict that endosperms with 2m:2p would be abnormally large, because of increased resource-acquiring activity by class-A paternal genes and reduced expression of class-B genes. However, these endosperms were aborted. Such abortions could be explained, within the framework of our hypothesis, either by an imbalance between the expression of class-A and class-B genes or by active abortion by the maternal sporophyte of ovules expressing unusually high resource-acquiring activity. There are still some puzzling features in Lin's data. Though endosperms with 3m:1p were subnormal, those with 6m:2p and 5m:2p and the same or smaller deviation from a 2:1 ratio were aborted.

Lin's evidence is especially convincing because he was able to study endosperms that had different maternal:paternal ratios but that were all interacting with the same maternal sporophyte. Other evidence comes from interspecific crosses in which seeds abort because of endosperm failure. In some cases, viable hybrids can be produced by altering the ploidy of one of the parents. This evidence usually cannot separate the effects of different maternal contributions to endosperm from the effects of different maternal sporophytes.

In crosses among *Solanum* (Solanaceae) species, the ploidy changes needed to produce viable seeds can be understood in a simpler way than by having special rules for each cross. Johnston et al. (1980) assigned species an endosperm balance number (EBN), which describes their behavior in crosses. Crosses were viable between species with the same EBN, but crosses between species with different EBN's showed abnormal endosperm development. However, if the ploidy of the male or female parent was adjusted to generate a 1:1 ratio of parental EBN's, normal endosperm development could be obtained. A similar coefficient can explain interspecific crossing rules in oats (Nishiyama and Yabuno 1978).

Two closely related diploids, *Solanum commersonii* (1 EBN) and *S. chacoense* (2 EBN), are normally intersterile. Nevertheless, Ehlenfeldt and Hanneman (1988) were able to produce a small number of diploid F_1 hybrids from a large number of interspecific pollinations (see their paper for the probable origin of these hybrids). Thus, the F_1 hybrids were heterozygous for those alleles determining the different EBN's of the parent species. Furthermore, the meiotic products of the hybrids would contain different combinations of the parental alleles. Crosses using the hybrids would be expected to produce neither consistent development nor consistent failure of endosperm but varying proportions of each. When hybrids were used as pollen parents in crosses with *S. chacoense* (2 EBN), about 50% of seeds aborted and the viable seeds were of small to average size. When *S. chacoense* was the pollen parent, most seeds aborted but viable seeds were of average to large size. In crosses of hybrids with *S. commersonii* (1 EBN), the outcomes were reversed: viable seeds were average to large with the F_1 as pollen parent, but small to average in the reciprocal cross. Taken together, the results are consistent with a positive relation between seed size and relative paternal activity, except that seeds are aborted when paternal activity is either very high or very low.

The interpretation of *Solanum* crosses in terms of species-specific EBN's would be interpreted by our model as follows. Over evolutionary time, different species evolve to have male genomes with different levels of activity in resource acquisi-

tion. However, within each species, this paternal activity comes into balance with the effects of the double maternal contribution. Since endosperms resulting from crosses between species often do not have the appropriate balance between paternal and maternal activity, defective endosperms can result. However, endosperm balance can be restored by appropriate changes in the ploidy of one of the parents. These features indicate that although different species maintain a similar balance between paternal activity and the effects of the double maternal contribution, this balance may be achieved at different levels of paternal activity.

SYNOPSIS

A characteristic feature of flowering plants is endosperm, a tissue with more doses of maternally derived than paternally derived genes. Endosperm is responsible for acquiring resources for offspring from mother plants. Recent hypotheses about the unusual genetic composition of endosperm have argued that because endosperm is more closely related to other offspring of the same mother than is the embryo, natural selection would cause the endosperm to be less vigorous than the embryo in acquiring provisions from the mother. However, since endosperm contains qualitatively the same alleles as the embryo with which it is associated (for monosporic gametophytes, which are the great majority), it has not been clear how an extra maternally derived allele could actually reduce the vigor with which a tissue sought to acquire resources. In this paper, we propose a mechanism by which this could happen.

At loci that encode proteins directly responsible for acquiring resources from the mother, parent-specific gene expression (PSGE) would be expected to arise, with strong expression of the paternally derived allele and little expression of the maternally derived allele. At these class-A loci, adding an extra copy of the maternally derived allele could not reduce the vigor with which the offspring sought to acquire resources from the mother. However, it can be assumed that there exist other class-B loci that are important to tissue functioning but not directly involved with acquiring resources from the mother. We further assume that total gene expression across the whole genome is restricted, such that increased expression at class-B loci has the effect of decreasing expression at class-A loci. Given these assumptions, we show that adding an extra maternally derived allele at each locus would moderate gene expression at class-A loci.

PSGE is therefore capable of explaining in general terms how the second maternal genome in endosperm nuclei might affect the endosperm's resource-acquiring behavior. The hypothesis also implies that triploid endosperms might have evolved from an immediate ancestor with one maternal and one paternal genome, rather than from an ancestor with two maternal genomes to which an extra paternal genome was added. Several aspects of the hypothesis are testable, and some supporting evidence already exists.

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